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Observations on the Electric Discharge of *Narcine brasiliensis* (Ölfers).

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Text-figures 1-4.

Narcine brasiliensis (Ölfers), in common with other members of the order Narcaciontes, shows marked electric power, as has been often noted. It gives a severe enough shock that fishermen, when they net it, avoid handling it alive, and Coles (1910) has reported being knocked down by its discharge. The utility of this power in the normal environment of the fish has not been studied. Its protective value would seem to be obvious, but if there are more subtle uses they await further investigation.

Heretofore observations on the electrical activity of this species have been made under rather fortuitous circumstances and the information given has been of necessity somewhat fragmentary, Bean & Weed (1911) and Breder & Springer (1940). In the hope of being able to make a more systematic study, the present work was undertaken in June, 1941, at the laboratory of the New York Aquarium at Palmetto Key, Florida. Electrical measurements were made on twenty live specimens, including fourteen adults, with both sexes represented, and six prematurely born young, belonging to two litters. These were born nearly at full term, with a small dependent yolk sac. A specimen from the first litter was observed about a quarter hour after birth. One from the other litter was some hours old at the time of the first observation. Electrical measurements were made on the mother of one litter just before birth and on the mother of the other litter within a day after birth. Thus the range of variation in the condition of the specimens included the chief phases in the life of the fish.

The discharge is produced by paired electric organs, similar to those described for the related and better known genus, *Torpedo*. They comprise in *Narcine* about one-sixth of the weight of the fish, which is roughly the same as the proportion found in *Torpedo occidentalis* but much less than that in *Electrophorus electricus*, where half the weight of the fish is in the electric organs. It has been remarked by Coates, Cox & Granath (1937) that the shape of the organs in the principal electric species is suited to produce a maximum output of power in the water they inhabit, whether fresh or salt. Thus the chief marine species have organs with their greater dimensions transverse to the axis of electric polarity, in contrast to the fresh water species, in which the organs are elongated parallel to this axis. An earlier similar observation was made by du Bois-Reymond, as noted by Gotch (1900). *Narcine* accords with this principle. The electric poles of the organs are their dorsal and ventral surfaces, and the smallest diameter of these surfaces is still several times larger than the average distance between them. The dorsal surface is positive, as in *Torpedo*. The polar surfaces are covered only by thin layers of connective tissue and skin. The outline of the organs is clearly visible on the ventral surface and visible also, though somewhat obscured by the spots in the skin, on the dorsal surface. (See Text-fig. 1.) The thickness of the organs decreases toward the periphery of the body from their inner edge, which is at the line of the gill slits.

In *Narcine*, as in *Torpedo*, the electric organs resemble honeycombs in their structure, the electroplaxes lying in piles of roughly prismatic shape, which extend from dorsal to ventral surface. Blood vessels supplying the electric organs lie in the sheaths of connective tissue which separate the prisms of electroplaxes.

The number of prisms of electroplaxes was counted in several specimens, and the counts are given in Table I. The count

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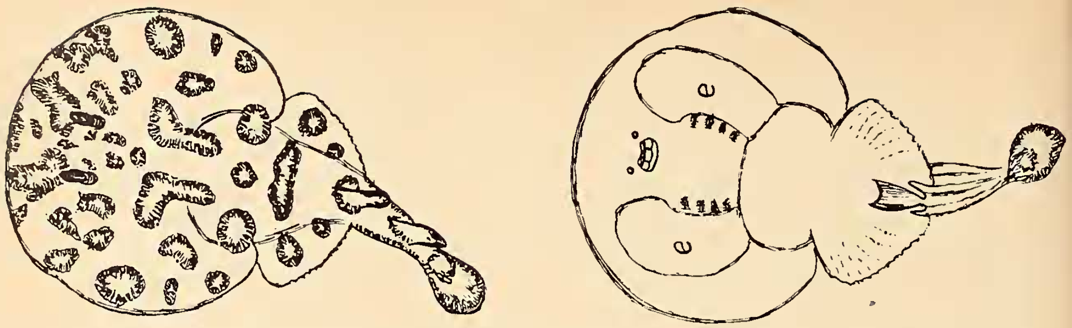


Text-fig. 1. Embryo *Narcine brasiliensis* (Ölfers). Dorsal and ventral views. "e" — electric organs. Yolk attachment omitted. Width of disc = 48 mm.

could in no case be made with precision, and in one of the embryo specimens the condition of the material caused a very large uncertainty. All counts refer to a single organ of the pair.

TABLE I.

Number of prisms of electroplaxes in one organ of various specimens.

Specimen	Counts	Average	
#5, adult male	356, 343	350	
#10, adult female	376, 388	382	Average for three
another adult	402, 416	409	adults, 380
#E5, embryo	267, 267	267	
another embryo	290, 340	315	Average for three
another embryo	264, 287	276	embryos, 286

It will be noticed that the lowest count for an adult is higher than the highest for an embryo, and the average of the embryos is only three-quarters that of the adults. If anything could be inferred from counts on so few specimens, it would be that the number of prisms increases during the growth of the fish, but much the more important factor in the growth is the increase by approximately nine-fold in the average area of cross-section of the prisms.

Counts were also made of the number of electroplaxes in one prism. Formalin was used as a fixative and is evidently not very satisfactory for this purpose. Fairly clear sections were obtained from two of the embryos, their organs being small enough for adequate penetration. With these specimens counts were obtained as shown in Table II.

Sections prepared from two adult specimens, #5 and #10 in Table I, were only clear enough for rough guesses of the number of electroplaxes in series. The electroplax boundaries were badly broken and displaced and the nuclei, the rows of which were found to be useful features for counting electroplaxes in the smaller organs, were not distinct in these. Such estimates as could be made gave no evidence of an increase in the number of electroplaxes in a prism during the growth of the fish after birth. The mean of two rough estimates of the number of electroplaxes in prisms of the two adult specimens was actually somewhat less than the mean of the counts from homologous prisms of the embryos.

In the development of the eye, *Narcine*

TABLE II.

Number of electroplaxes in one prism of the organs of various specimens.

Specimen	Position of prism in organ	Counts	Average
#E5, embryo	short prism near outer edge	180, 178	179
	long prism near inner edge	314, 296	305
#E4, embryo	short prism near outer edge	321, 273, 270, 288	288
	long prism near inner edge	483, 481	482

presents a contrast with *Electrophorus*. The eyes of *Electrophorus* deteriorate with increasing age, and it has been supposed by Coates, Cox & Granath (1937) that the deterioration is an injury produced by the electric discharge. The eyes of *Narcine*, like those of some other marine electric species, are very near the electric organs, but they do not seem to be inferior to the eyes of other rays. It seems reasonable to suppose that some difference in the two species or in the electrical characteristics of the waters they inhabit might make the electric discharge injurious to the eye of one but not to the eye of the other. If so, an understanding of this difference would be of interest.

The first two specimens of *Narcine* obtained alive in the present work sustained an injury to the eye of a quite different sort from that just considered but of some interest in another connection. These specimens were left in a "live car" from which a miscellaneous collection of fishes had been removed. Those remaining, besides the two *Narcine*, were three flounders, *Paralichthys albiguttus* (Jordan & Gilbert), and, by inadvertence, two pin fish, *Lagodon rhomboides* (Linnaeus), overlooked because of their small size. The first intimation we had of the presence of the pin fish was that the next day both *Narcine* were without eyes. It is well known that the pin fish, along with other species, has a tendency to pick at the eyes of fish which lie prone on the bottom, attracted apparently by the movement and brightness of the eyes. Inasmuch as the unprotected flounders were not injured, it was distinctly surprising to find that in spite of their electric power the *Narcine* were unable to protect themselves. It may be that they soon exhausted their ability to discharge electricity, as they apparently do, and then in confinement were at a disadvantage, since they are notably less alert than the flounders. Another consideration is that *Narcine* is seemingly reluctant to discharge. Certainly such injury to the eye would be expected to call forth all protective measures, but perhaps the injury was inflicted before the electric discharge could be produced.

The discharge is generally accompanied by muscular activity similar to that described by Coates & Cox (1942) in *Torpedo occidentalis* and much more pronounced than the slight tremor which is sometimes seen to accompany the discharge of *Electrophorus*. This activity, it was observed, varied somewhat from fish to fish and from one time to another, but it tended to follow a fairly regular sequence. When about to discharge the fish usually turns up the edges of the pectorals, so as to form an upstanding frilled edge. Next there follow muscular contractions running down the back and, at the moment of discharge, an almost tetanus-like quiver goes through the whole fish. This series of events may or may not be accompanied by swimming movements of more or less vigor. Usually if these occur they start at about the time of discharge and can be taken to indicate that more discharges will follow quickly. After the effort is over, the fish lies quiescent and does not repeat either electrical or muscular activity for some little time. After several efforts of this kind the fish gradually becomes limp and flaccid and requires a considerable period of rest before more discharges can be elicited.

The observations just described were made along with the electrical measurements. To make these measurements the fish was removed from the water and laid on an aluminum plate which thus made electrical connection through the wet skin of the fish with the ventral or negative poles of the electric organs. A smaller aluminum plate covered and made connection with the dorsal or positive surface of the organ on one side, right or left. The two plates were joined by wires to the terminals of a cathode ray oscillograph, which could thus be used to measure the voltage developed between the two poles of the organ. One of us manipulated the fish while the other made the electrical measurements. A close check on the association of the muscular and electrical activities of the fish could be made by the manipulator of the fish alone, whether or not he observed the oscillographic screen, because he could practically always feel the shock of the discharge in the hand with which he held the fish and the upper electrode in place. The hand was protected by a rubber glove, but the dampness of its surfaces, inside from perspiration and outside from the fish, permitted a distinctly appreciable current to pass. In fact it was necessary to keep two pairs of gloves in service, one drying while the other was in use, to prevent the passage of a cramping current. The sequence of muscular and electrical activity was regular enough that the manipulator of the fish could generally foretell a few moments in advance that the discharge would be produced, a feature of some convenience in the observations.

The exact significance of these muscular movements is not clear. Possibly the strong quiver at the instant of the discharge is evidence that the fish receives some shock from its own current. The tremor sometimes seen in *Electrophorus* also occurs at the instant of discharge and would seem thus to be the counterpart of this phase in the muscular sequence of *Narcine*. In *Electrophorus* the quiver can be intensified locally by the use of small electrodes concentrating the current in a chosen region, and it thus appears to be simply the muscular contraction caused by shock. Therefore the intense quiver in *Narcine* may also have this explanation.

For the sequence as a whole, the most likely interpretation would seem to be that its various phases are the different parts of an effort to escape. The curling and frilling movements appear to be an exaggeration of those used to flurry sand over the back, a habit common to most rays, which in a state of nature serves to blanket them from vision. This failing, an electric discharge should protect, but finally, this also failing, flight, as shown in the swimming movements of the muscular sequence, would be resorted to as in most animals when the special defense reactions do not produce the customary result.

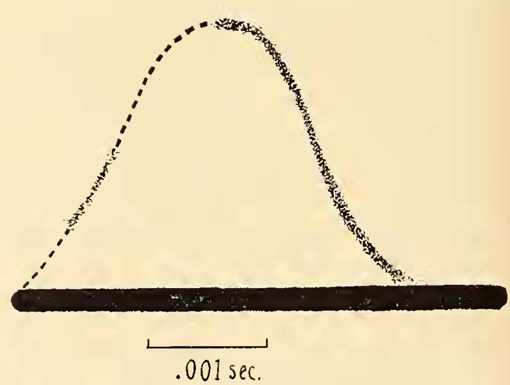
These fish do not give off their discharge readily at best, and at no time in netting them from the live car in which they were kept were they noted to do so. In fact after a time it was found that they could be transferred by the bare hands without danger of a shock. When they were in place for the observations, it was usually necessary to prod, lightly pinch, or otherwise annoy them in order to elicit the desired discharge. Various methods were tried in order to obtain a quick and sure stimulus. These included pinching the caudal fin, stroking the back, bending the tail and others. Each seemed to give promise when first tried but soon failed, and it finally developed that a new stimulus was more effective than any one kind often repeated. After the fish had discharged several times, it would sometimes carry through the pattern of muscular activity which normally precedes the discharge, but without discharging.

The electric organs of *Narcine*, like those of other electric species, discharge intermittently in brief pulses, which follow one another to form a train of variable length. One or a few such trains constitutes the discharge associated with the muscular sequence which has been described. A faint photograph of the oscillographic traces of such a train, showing the regularity of the peak voltages and of the interval between

Text-fig. 2. Oscillographic trace showing the train of pulses in the discharge.

pulses, is copied in Text-fig. 2. (Only faint photographic traces were obtained because the power supply was not quite enough for the oscillograph.) The train shown is typical insofar as there is a type, but wide variations were noticed. The first of the young fish to be observed, about 15 minutes after a premature birth, gave from two to five pulses at irregular intervals in a train. The young of the second litter, also premature but some hours old at the time of observation, gave discharges in better formed trains of about five pulses to the train. There were more pulses still in the trains produced by adults, and the interval was regular enough that when the discharge passed directly through a telephone receiver it produced a short but clear musical note. One specimen, a gravid female, gave trains of one hundred or more pulses, as well as the eye could reckon them, but this behavior was exceptional.

Text-fig. 3 shows the form of a single pulse on a more open time scale than that of Text-fig. 2. This figure also is drawn from a faint photograph, but the dotted portion is supplied from memory of visual observation. The trace was obtained with the electric organ as nearly as possible on "open circuit," no significant current being drawn except that which flowed in the circuit made through the body of the fish. A comparison of this trace with those obtained similarly by Coates & Cox (1942) from *Torpedo occidentalis* and *Electrophorus electricus* shows that the pulse form of *Narcine* resembles that of *Torpedo* rather than that of *Electrophorus*, as might be expected on a basis both of relationship and of structural detail.



Text-fig. 3. Oscillographic trace of a single pulse.

The synchronization of the discharge in the two electric organs of one fish was tested by the method Coates & Cox (1942) employed with *Torpedo*. One organ was connected, instead of the timing circuit, to the oscillograph to produce the horizontal motion of the electron beam, while the other organ caused the vertical motion as usual. If the two organs discharge in exact synchronism, the resulting trace is a straight line; otherwise it is a loop the width of which shows the time lag between the pulses in the two organs. One newborn specimen and several adults were observed in this way. Observations of the same kind, but with small electrodes each covering only a part of the organ on one side, were also made in order to see if the pulse were simultaneous in all parts of the same organ. The result of all these observations was to show that all parts of both organs discharge in almost exact synchronism. Occasionally the synchronization was not quite perfect and the pulse from one organ followed that from the other by about .0001 second, or one thirtieth the duration of the pulse. Even these deviations were more frequently observed after the fish had discharged a number of times, and they may therefore be signs of fatigue.

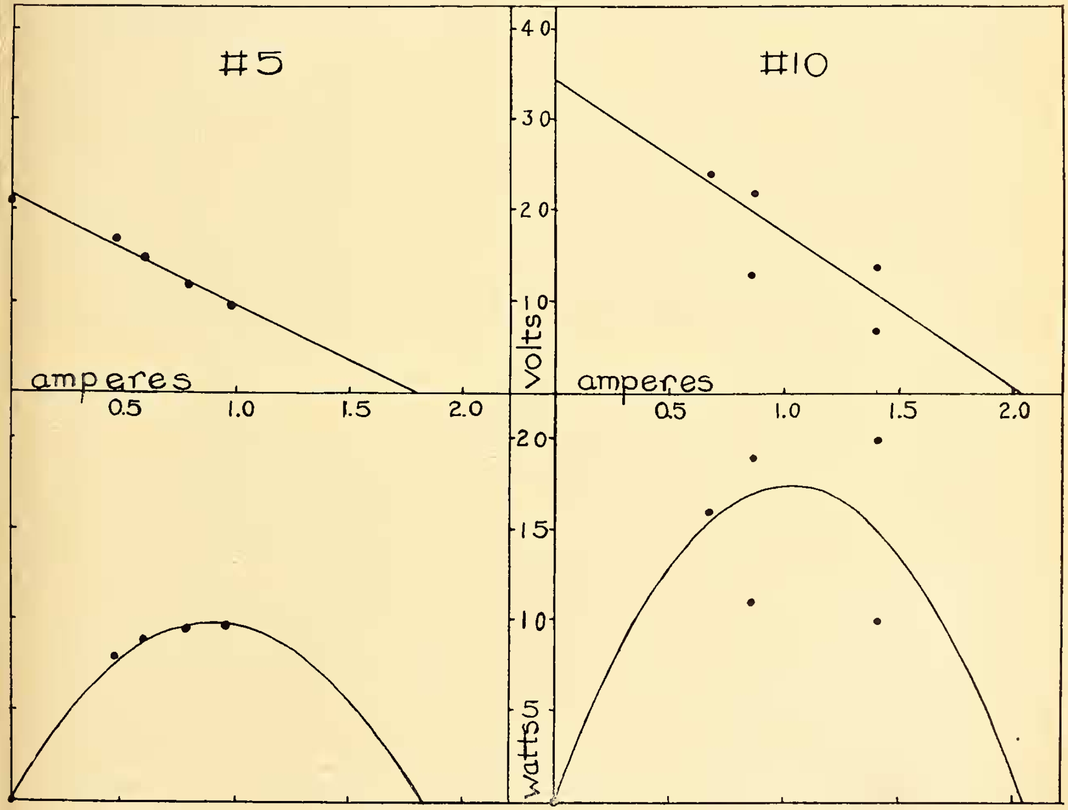
Many measurements were made, visually with the oscillograph, of the peak voltages of the pulses produced by the various specimens. Voltages were measured both on open circuit and when current was drawn from the organ through known external resistances. The voltage being V and the resistance R, the current I flowing in the external resistance is given by I = V/R, and the power P by P = VI. These measurements and computations are shown for two specimens in Table III.

TABLE III.

Voltage, current and power at peak of discharge for various values of external resistance.

Specimen	R ohms	V volts	I amperes	P watts
#5	∞ *	21	0	0
	35.8	17	0.47	8.0
	25.5	15	0.59	8.9
	15.3	12	0.78	9.4
	10.3	10	0.97	9.7
#10	∞ *	37	0	0
	35.8	24	0.67	16
	25.5	22	0.86	19
	15.3	13	0.85	11
	10.3	14	1.4	20
	5.0	7	1.4	10

* Open circuit.



Text-fig. 4. Graphs of voltage and power against current, all at the peak of the discharge.

These data are plotted in Text-fig. 4. It will be seen that the graph of voltage against current is quite near to a straight line with specimen #5. With specimen #10 the points scatter widely and no smooth graph could be drawn to pass near all of them. These two fish gave, respectively, the most consistent and the most erratic data obtained. In general we find, not only with *Narcine*, but also with *Electrophorus* and (though with fewer observations) with *Torpedo*, that the more we can avoid tiring the fish the more nearly the plotted values of voltage and current determine a straight line.

The maximum voltage of the organ is produced when the external current is zero, and it is thus the intercept of the plotted line on the axis of voltage. If there were no circuit made through the body of the fish, so that the internal current was zero as well as the external current, then the maximum voltage would be equal to the electromotive force of the organ. It seems likely that the electromotive force is actually not much greater than the maximum voltage.

The two graphs in the lower half of Text-fig. 4 show the power delivered to the external circuit for different values of the current. These graphs are plotted by the equation $P = VI$ from the values of V and I taken from the graphs above. The plotted points are those from Table III computed by the same equation. The power is maximum when the voltage and current have half their maximum values.

Table IV summarizes the results obtained with the whole group of adult specimens by the methods illustrated with specimens #5 and #10. The values of maximum power given in this table are reckoned for both organs discharging together. Thus the values given for specimens #5 and #10 are twice those shown in Text-fig. 4.

As is also true with *Torpedo*, the electromotive force and power of the electric organs of *Narcine* decline rapidly as the physical condition of the fish is impaired by fatigue or other causes. For this reason the maximum values of voltage and power shown in Table IV may be more characteristic of the normal specimen than the average values are.

The observations obtained with the newborn specimens were much less complete. The peak voltage of one of the first litter was measured and found to be 6 volts. The voltage was so much lowered by connection to even the highest of our measured resistances that the maximum power was not accurately measured. It was estimated as about 0.1 watt for the two organs of this fish discharging together.

The second litter was born in a tank in which the mother was being brought to the laboratory. Measurements of the voltage on open circuit were made promptly. One fish showed a peak voltage around 22 volts, three between 13 and 16 volts, and one around 3 volts. This last was pale in color, a sign of poor condition, and it died within a few hours. Measurements were repeated on three of the fish, and the voltages were found somewhat lower on the average than at first. No determination of the power was made. The highest voltage measured with one of these newborn fish, 22 volts, being almost equal to the average for the adults, it seems that the electromotive force of the organ does not increase proportionately, if it increases at all, with the growth of the fish. It has already been noted that the number of electroplaxes in series does not increase proportionately with growth and may, as far as we can tell, be fixed at birth.

The number of electroplaxes is not well known, however, for any of our adult speci-

TABLE IV.

Dimensions, weight, peak voltage on open circuit and maximum power of various specimens.

Specimen	Sex	Length cm.	Width cm.	Weight gm.	Peak voltage, open circuit volts	Maximum power watts
1	m	25	13	—	18	—
3	m	24	12	230	15	7
4	f, gravid	32	17	450	23	—
5	m	26	13	250	21	19
6	m	28	14	300	29	19
7	f	25	14	270	21	11
9	m	26	13	210	25	16
10	f	27	14	280	37	35
11	f	26	14	270	14	5
12	f, gravid	33	18	650	27	25
average	m	26	13	248	22	15
"	f	29	15	gravid, 550 others, 273	24	19
"	m and f	28	14		23	17

mens. It is impossible therefore to determine with any accuracy the electromotive force per electroplax. Probably the right order of magnitude will be found by taking 30 volts as the electromotive force of 300 electroplaxes in series, which gives 100 millivolts as the electromotive force per electroplax. Values on both sides of this are observed in *Electrophorus*.

The weights of the electric organs and their cross-sectional areas perpendicular to the direction of the current, parallel, that is, to the dorsal and ventral surfaces, were measured for specimens # 5 and #10. From these and the electrical measurements already given we find the maximum power delivered externally per gram of tissue and the current per square centimeter flowing through the tissue at maximum power.

These values are in Table V below. Those reported for *Torpedo occidentalis* are given for comparison. In each case, the weight, power and current are those of both electric organs.

Table V.

Specific current and power of *Narcine* and *Torpedo*.

Specimen	Total weight gm.	Weight of electric organs gm.	Fraction of weight in electric organs	Maximum power watts	Maximum power per gm.	Current at maximum power amperes	Cross-sectional area of organs sq. cm.	Current per sq. cm.
Narcine								
#5	250	42	0.17	19	0.5	1.8	44	0.04
#10	280	52	0.19	35	0.7	2.1	41	0.05
Torpedo	25,000	4,000	0.16	6,000	1.5	60	500	0.12

We wish to express our thanks to the Department of Biology of New York University at University Heights for technical assistance in the preparation of sections of the electric tissue.

Summary.

The adult *Narcine brasiliensis* used in this study has an average length of 28 cm., an average width of 14 cm., and an average weight around 270 grams, the female being slightly larger than the male. About one-sixth of its weight is in two electric organs, which extend from dorsal to ventral skin, the dorsal surface being the positive pole. Each organ is a parallel array of 300 to 400 prisms of electroplaxes, with something like 300 electroplaxes in series in one prism. The growth of the organ is more an enlargement of the electroplaxes than an increase in their number; neither the number of prisms nor the number of electroplaxes in one prism increases greatly after birth. The electromotive force per electroplax is of the order of 100 millivolts but varies widely according to the condition of the fish. The electric power is well developed at birth.

The two organs discharge simultaneously in a train of pulses in rapid succession. Each pulse lasts about .003 sec., and the number in one train varies from about five to (exceptionally) one hundred or more. The discharge is accompanied by a muscular sequence which appears to be made up of motions of concealment and flight and perhaps self-shock. The power released externally attains in the discharge an instantaneous value of about 0.7 watt per gram. The current density in the organ when this power is developed is about .05 ampere per sq. cm.

Comparison with other electric fish shows electrical resemblances between *Narcine* and *Torpedo* as marked as their morphological resemblances. The electrical differences are only those to be expected from the difference in size. Also, in every respect in which one of these fishes shows a difference in electrical characteristics from *Electrophorus*, the other shows a difference of the same sort.

Literature Cited.

Bean, B. A. & Weed, A. C.
1911. An electric ray and its young from the west coast of Florida. *Proc. U. S. Nat. Mus.*, 40:231-232.

Breder, C. M., Jr. & Springer, S.
1940. On the electric powers and sex ratios of foetal *Narcine brasiliensis* (Ölfers). *Zoologica*, 25 (26):431-432.

Coates, C. W. & Cox, R. T.
1942. Observations on the electric discharge of *Torpedo occidentalis*. *Zoologica*, 27 (5):25-28.

Coates, C. W., Cox, R. T., & Granath, L. P.
1937. The discharge of the electric eel, *Electrophorus electricus* (Linnaeus). *Zoologica*, 22 (1):1-32.

Coles, R. J.
1910. Observations on the habits and distribution of certain fishes taken on the coast of North Caroline. *Bull. Amer. Mus. Nat. Hist.*, 28:337-348.

Gotch, F.
1900. The physiology of electric organs. In Schafer, E. A., A Text-book of Physiology. London, 2:561-591.